

Biological Report 5
March 1993

Vole Management in Fruit Orchards

By

Mark E. Tobin and Milo E. Richmond

U.S. Department of the Interior
Fish and Wildlife Service
Washington, D.C. 20240

Contents

	Page
Abstract	1
Biology	2
Identification	2
Niche Separation Within Orchards	3
Activity Cycles	4
Reproduction and Life Span	4
Social Behavior	5
Feeding Behavior in Apple Orchards	5
Diet	5
Damage to Apple Trees	6
Control	7
Cultural Techniques and Orchard Management	7
Monitoring Techniques and Action Thresholds	10
Lethal Techniques	11
An Integrated Approach	13
Acknowledgments	14
References	14

Vole Management in Fruit Orchards

by

Mark E. Tobin¹ and Milo E. Richmond

U.S. Fish and Wildlife Service
New York Cooperative Fish and Wildlife Research Unit
Cornell University
Ithaca, New York 14853

Abstract. Meadow voles (*Microtus pennsylvanicus*), pine voles (*M. pinetorum*), and montane voles (*M. montanus*) cause significant economic damage in apple orchards throughout the eastern United States and in a few northwestern states where apples are grown commercially. By girdling the bark and roots, these rodents kill trees, reduce yields, and prolong the time for new plantings to come into production. We describe the identification, ecology, and behavior of voles in apple orchards, evaluate the types, extent, and magnitude of losses inflicted by these pests, and describe measures for reducing damage. Effective control requires a species-specific program that integrates cultural and chemical strategies aimed at reducing invasion, reproduction, and survival of voles in apple orchards. Frequent, close mowing of ground vegetation during the growing season and establishing a vegetation-free zone under the canopy of orchard trees reduces carrying capacity for vole populations. Periodic inspection for signs of reinvasion or repopulation allows application of controls before vole populations increase and significant damage occurs. When pest populations build up, toxic baits quickly provide cost-effective reduction. Proper selection, timing, and application is essential for obtaining best results with rodenticides.

Key words: Animal damage control, apples, fruit, orchards, girdling, *Microtus*, voles, field mice.

Voles are microtine rodents, a large group distributed widely in Europe, Asia, and North America. There are 71 species of voles and lemmings worldwide, and 23 species in North America (Hoffmann and Koepl 1985). In the western hemisphere, voles can be found from Central America to the high arctic and from sea level to alpine forests and meadows. Microtines reach their greatest densities in temperate grasslands and arctic meadows.

Three species of voles cause significant economic damage by feeding on apple trees (*Malus domestica*) in commercial orchards. Meadow voles (*Microtus pennsylvanicus*), the most widespread of

North American voles, occur throughout most of the northern United States in habitats that range from low moist swamps and fields to high grasslands and forests. Pine voles (*M. pinetorum*) are restricted to the eastern half of the United States in a variety of habitats. Both meadow and pine voles are major pests in apple orchards throughout the eastern half of the country. Montane voles (*M. montanus*) are found primarily in valleys and grassy meadows of the mountainous Great Basin and are of concern to orchardists in valleys of the Columbia River and its tributaries in eastern Washington state.

We describe the identification, ecology, and behavior of voles in apple orchards, evaluate types, extent, and magnitude of losses inflicted by these pests, and describe available measures for reducing damage by voles.

¹ Present address: U.S. Department of Agriculture, Denver Wildlife Research Center, P.O. Box 10880, Hilo, Hawaii 96721.

Biology

Identification

Names of voles and other mammals discussed follow the nomenclatural summary of Banks et al. (1987). Adult meadow voles, sometimes referred to as meadow mice or field mice, have relatively long fur that is dark brown mixed with black on the back and dusky gray on the belly (Fig. 1). Long guard hairs interspersed with denser, softer underfur give the pelage a coarse texture. The feet and tail are dusky above and pale below, and the tail is indistinctly bicolored. Mature meadow voles weigh 28.0 to 70.0 g (1.0 to 2.5 ounces) and vary in length (snout to tail tip) from 124 to 195 mm (4.9 to 7.7 inches). Tail length, which is more than twice the length of the hind foot, readily distinguishes them from pine voles. Newborns are naked and have dark-pigmented back skin and pink under-

sides. At 9 or 10 days of age meadow voles acquire juvenile pelage, when the pink skin becomes hidden as dark fur covers the body. Adult pelage is acquired after about 8 weeks of age.

Adult pine voles, also known as pine mice and woodland voles, can be distinguished easily from adult meadow voles in smaller size, reddish-brown to chestnut-brown coat color, and anatomical features adapted to subterranean life (Fig. 2). These adaptations include stocky body shape, small eyes and ears, short, soft fur lacking guard hairs, and tail length less than hind foot length. Mature pine voles weigh 22 to 37 g (0.8 to 1.3 ounces) and measure 88 to 132 mm (3.5 to 5.2 inches) from snout to tail tip. Adults are dull chestnut above, paler on the sides, and silvery to slate gray on underparts. Winter pelage is darker than that of summer (Hamilton 1938). Like meadow voles, pine voles go through juvenile and postjuvenile molts before acquiring adult pelage.

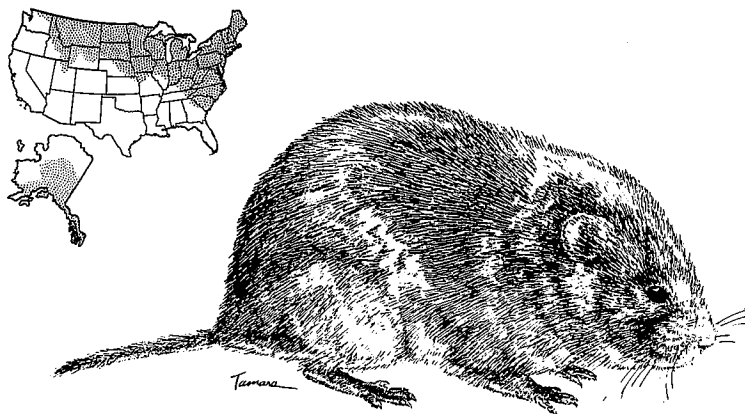


Fig. 1. Meadow vole, *Microtus pennsylvanicus*; shading on map inset represents geographic distribution in Alaska and the conterminous United States.



Fig. 2. Pine vole, *Microtus pinetorum*; shading on map inset represents geographic distribution.



Fig. 3. Montane vole, *Microtus montanus*; shading on map inset represents geographic distribution.

Adult montane voles are grayish brown to blackish above and whitish on the belly (Fig. 3). The nose and ears are frequently darker than the rest of the body. The feet are usually dusky. Most individuals have a nearly uniformly colored tail, although some have a more or less bicolored tail that is dark brown to buff gray above, sometimes with a reddish tinge, and dark gray beneath. Mature montane voles weigh 28.0 to 85.0 g (1.0 to 3.0 ounces) and measure 132 to 206 mm (5.2 to 8.1 inches) from snout to tail tip. The tail length usually is less than one-third of the length of the head and body. Table 1 outlines some major identification and ecological characteristics distinguishing meadow, pine, and montane voles.

Niche Separation Within Orchards

Meadow voles and pine voles inhabit the same orchards throughout much of the eastern United States, although the two species seem to prefer slightly different types of orchards (Stockrahm 1985). Meadow voles are associated with grassy orchards with abundant vegetative cover or ground litter. Meadow vole populations usually increase dramatically in poorly managed or abandoned orchards that have rank growth of grasses. Pine voles also seek areas with dense ground cover, but prefer broad-leaved plants rather than grasses. Pine voles occur most often in older orchards extensive canopies shading the ground.

Meadow voles are most active above the ground, as evidenced by surface trails through the vegetation. These runways are 2.5 to 5.0 cm (1 to 2 inches) wide and are often littered with droppings and grass cuttings. Meadow voles usually

build their intricate grass nests on the ground surface, but occasionally they occupy the underground burrows of other animals.

Pine voles spend much time in underground burrow systems 7.5 to 10.0 cm (3 to 4 inches) deep, and in extensive subsurface trail systems 3 to 6 cm (1 to 2 inches) beneath the litter layer or ground surface. Compared with those of meadow voles, trails used by pine voles are small and usually kept clean of grass cuttings and other debris. Pine vole trails typically measure about 1.9 to 2.5 cm (0.75 to 1.0 inches) wide. Openings to the surface from underground tunnels and dirt piles excavated from burrows also attest to the presence of pine voles. Pine voles frequently build their nests near the bases of trees at a depth of 7.5 to 30.0 cm (3.0 to 11.8 inches) below the surface of the ground.

The distributions of meadow voles and montane voles overlap extensively in the western United States, but social interactions and divergent habitat preferences reduce competition between these species (Koplin and Hoffmann 1968; Stoecker 1972; Douglass 1976). Meadow voles rarely are found in western apple orchards, where montane voles are the primary microtine pest. Occasionally longtail voles (*M. longicaudus*) damage apple trees (M. Godfrey, Wildlife Consultants, Inc., Des Moines, Iowa, personal communication). Northern pocket gophers (*Thomomys talpoides*) also inhabit western orchards and girdle roots of apple trees extensively. Fan-shaped mounds of dirt excavated from underground tunnels distinguish the presence of pocket gophers.

Montane voles build subterranean nests and also utilize underground burrows of pocket gophers and other species (Jannett 1982). Montane voles

Table 1. *Distinguishing characteristics of meadow vole (Microtus pennsylvanicus), pine vole (M. pinetorum), and montane vole (M. montanus).*

Characteristic	Meadow vole	Pine vole	Montane vole
Length (head and body)	90–125 mm (3.5–5 inches)	70–105 mm (2.8–4.2 inches)	102–140 mm (4–5.5 inches)
Tail length	35–65 mm (1.4–2.6 inches) at least twice the length of the hind foot	15–25 mm (0.6–1.0 inches), less than or equal to the length of the hind foot	30–65 mm (1.2–2.6 inches), at least twice the length of the hind foot
Adult fur	Coarse, dark brown mixed with black	Soft, auburn, lacking guard hairs	Coarse, grayish brown to black
Eye size	Large	Small	Large
Ear appearance	Large	Inconspicuous	Inconspicuous
Nest placement	Usually aboveground, but occasionally in shallow burrows	In burrows, usually less than 30 cm (1 foot) deep	In burrows
Sociality	Females maintain exclusive territories during breeding season, males mobile; social during winter	Family units maintain year-round exclusive territories	Both sexes maintain separate territories during breeding season; social during winter
Food	Grasses, sedges, seeds, grain, bark, some insects	Bulbs, tubers, seeds, bark	Grasses, sedges, seeds, grain, bark, some insects
Damage	Girdle tree trunks at or near ground surface; may girdle higher under cover of snow; sometimes damage roots	Girdle crown and roots	Girdle trees both above and below the ground surface; damage may extend higher under cover of snow

spend most of their time underground during late spring and summer to avoid heat, but probably feed aboveground more during wet and cool times of the year (L. Askham, Washington State University, Pullman, Wash., personal communication).

Activity Cycles

Voles spend much time seeking food to support their high metabolism. They remain active throughout the year, (i.e., they neither hibernate nor estivate), although activity varies seasonally, especially in areas that have extreme seasonal variations in climate. In severe northern climates, voles cache food for use during winter and conserve heat by living in communal nests (Hatt 1930; Webster and Brooks 1981; Madison 1984; Madison et al. 1984). Considerable movement occurs under protective snow cover (Madison et al. 1984). During hot summer months, voles avoid high surface temperatures by diminishing movement away from the nest and confining activity to early morning and evening (Fitch 1954; Benton 1955; Getz 1961; Gentry 1968; Paul 1970).

Voles are usually most active at dawn and dusk (Hamilton 1937; Paul 1970), although they may be

about at any time of the day or night (Johnson and Johnson 1982). Factors such as season, weather, snow cover, predation, and local habitat conditions undoubtedly influence diurnal activity. Voles typically leave their nest every 2–4 h to forage and for other activities. However, individuals in a population may not be synchronously active (Ambrose 1973; Madison 1985).

Reproduction and Life Span

Voles are short-lived, prolific animals. Although individuals rarely live more than a year (Getz 1960; Gourley 1983; Anthony et al. 1986), their populations have astonishing potential for increasing rapidly. The periodic buildup and decline of rodent populations, including the extremes shown by arctic lemmings, have long intrigued biologists (Piper 1909; Elton 1942; Pitelka 1957; Chitty 1960; Hestbeck 1986).

Reproduction occurs in any season (Benton 1955; Horsfall 1963; Goertz 1971; Jannett 1984), but is usually limited to times when food is abundant and climatic conditions are favorable (Hamilton 1938; Cengel et al. 1978; Batzli 1986). Studies have demonstrated the importance of green plant

tissue (Negus and Berger 1977; Negus et al. 1977), specifically the compound 6-methoxybenzoxazolinone (Berger et al. 1981, 1987; Sanders et al. 1981; Korn and Taitt 1987), for stimulating voles to breed. Reproductive activity typically reaches a peak in spring, summer, and fall (Benton 1955; Horsfall 1963; Miller and Getz 1969; Valentine and Kirkpatrick 1970; Cengel et al. 1978; Anthony et al. 1986), but in some areas decreases during hot summers (Goertz 1971).

Meadow voles are promiscuous breeders (Madison 1980; Webster and Brooks 1981; Oliveras and Novak 1986). Among reproductively active individuals, home ranges of males are larger than those of females and typically overlap the ranges of other reproductively active voles of both sexes (Ostfeld et al. 1988). Females, however, maintain breeding territories that are mutually exclusive from those of other reproductively active females. Females reach sexual maturity as early as 3 weeks of age and, after a gestation period of 21 days, they give birth to litters that average four to seven young (Dobson and Meyers 1989; McShea and Madison 1989). Some litters have been known to contain as many as 12 pups (Johnson and Johnson 1982). Females may give birth to a second litter as soon as 21 days after birth of the first litter (McShea and Madison 1989). Captive meadow voles have produced as many as 17 litters in 1 year (Bailey 1924), although 3-4 litters per year is probably more common in the wild (Burt and Grossenheider 1976).

The mating system of montane voles is variable; it encompasses facultative monogamy at low population density and polygyny (i.e., males mate with more than one female) at high density (Jannett 1977, 1982). Females apparently nest with only one male; home ranges of territorially dominant males overlap those of one or more females (Jannett 1977). Average litter size varies between five and seven young (Negus and Pinter 1965; Hasler 1975; Innes 1978). Females can produce litters at 21-day intervals (Jannett 1977).

Pine voles have a lower reproductive rate than most other voles, perhaps as an adaptation to their relatively secure subterranean lifestyle. Pine voles take longer to reach reproductive maturity, have a longer gestation period, and give birth to smaller litters. Pine voles rarely breed before they are 4 weeks of age (Schadler and Butterstein 1979; Gourley 1983; Anthony et al. 1986), and females gestate about 24 days before giving birth to two or three young (Hamilton 1938; Goertz 1971; Anthony et al. 1986).

Social Behavior

The social behavior of meadow voles varies seasonally (Madison and McShea 1987). During the breeding season, contact among adults is minimal except in males competing for access to estrous females (Madison et al. 1984). Males take little part in rearing offspring (Oliveras and Novak 1986). During winter, animals become more tolerant and live in communal groups comprising as many as seven individuals (Madison et al. 1984).

Except for courtship and mating, male and female montane voles interact little during the breeding season. Both sexes defend territories against intrusion by others of the same sex (Jannett 1977, 1980; McGuire and Novak 1986). Members of a breeding pair occupy separate nests during the breeding season (Jannett 1977, 1982) but may share living quarters during the nonbreeding season (Madison 1984). Paternal care of young is essentially nonexistent (McGuire and Novak 1986). Females may have extended families that include the young from one or more litters (Jannett 1977).

In contrast to most voles, pine voles live in extended family units that maintain exclusive territories all year (Renzullo and Richmond 1982). Each group typically consists of a pair of breeding adults and two to four offspring, although occasionally more than one reproductively active male is included (FitzGerald and Madison 1983; Oliveras and Novak 1986). Males assist in building and maintaining nests and tunnels, but females handle most other duties of raising litters.

Feeding Behavior In Apple Orchards

Diet

Preferred foods for voles usually are characterized by high water or energy content, or presence of specific nutrients, such as nitrogen, calcium, phosphorus, and sodium (Meade 1975; Brooks and Struger 1984; Batzli 1985). Meadow voles forage almost exclusively aboveground on fresh leaves and stems of a wide variety of grasses and broadleaf plants (Batzli 1985). Pine voles feed mostly below the surface on tubers, roots, and underground stems (Hatt 1930; Benton 1955; Cengel et al. 1978). All three species of voles eat fruit when it is available and also take seeds, woody materials, and bark when green foods are of

low quality or in short supply. During fall, voles collect and store fruits, stems, leaves, and underground roots and bulbs of numerous plants for use during winter (Hamilton 1938; Gates and Gates 1980). These caches, sometimes measuring up to a gallon in volume (Hamilton 1938), formerly were robbed by native Americans for food during winter (Bailey 1924).

Damage to Apple Trees

When preferred foods are scarce, as in winter, voles may gnaw the trunks and roots of apple trees for the underlying phloem and cambium tissue. The resulting damage interferes with subsequent transport of nutrients and photosynthate between the roots and aerial portion of the tree, and increases the chances of infection by root pathogens (Byers 1984). Damage by voles is most severe during long, harsh winters, when alternative foods are scarce. Prolonged snow cover insulates voles from inclement weather, protects them from predators, and allows extensive girdling of the tree cambium. Damage that occurs belowground or under snow often escapes notice until the tree dies or is irreversibly damaged.

Meadow voles eat the bark of trees above ground surface and, where snow cover allows (Fig. 4), damage may extend more than a foot (0.3 m) up the trunk (Silver 1924; Caslick and Decker 1978). In contrast, pine voles girdle the crown and roots of trees at or below the surface of the ground. Montane voles girdle both above-ground bark and roots (Godfrey 1987). In trees with severe root damage, sometimes all rootlets and smaller (pencil-sized) roots are completely eaten or removed; the taproot may appear as though it were sharpened in a pencil sharpener (Hamilton 1938; Richmond et al. 1987). Sublethal symptoms of root girdling in orchard trees may include one or more of the following: abnormally yellowish leaf color (Fig. 5), pinkish bark (from reduced nitrogen uptake), overall poor tree vigor, reduced fruit yield, and prolonged time required for newly planted trees to come into production (Pearson 1976).

Economic losses from vole damage to apple trees are difficult to estimate. Differences among varieties and ages of trees, changing market prices and production costs, varying land values, difficulty in quantifying effects of vole girdling and calculating replacement costs all complicate the task of measuring losses. Nonetheless, such losses have been documented. Byers (1974) estimated that 5.6% of



Fig. 4. An apple tree girdled by meadow voles.

the market value of apples grown in the United States was lost to pine vole damage, resulting in annual losses of \$40 million. An early report (Silver 1924) described an orchard near New York City in which voles caused a \$10,000 tree loss. Phillips et al. (1987) surveyed apple growers in the mid-Hudson Valley of New York and estimated that total costs associated with application of vole control measures, replacement of trees killed by voles, and reduced production of trees damaged by voles averaged \$44/ha (\$108/acre) per year.

A few investigators have attempted to measure the effects of vole activity on the growth and productivity of apple trees. Pearson and Forshey (1978) found that McIntosh, Red Delicious, and Rome Beauty apple trees girdled by voles had 36–59% less terminal shoot growth than noninjured trees. Forshey et al. (1984) studied confined populations of pine voles and estimated that, in 10-year-old McIntosh trees, damage of high population levels reduced terminal shoot growth by 92%, total leaf area by 73%, and crop yield by 65%. Moreover, 58% of the apples produced were under-



Fig. 5. Apple tree (left) girdled by pine voles. Note the pale leaves and sparse foliage.

sized. Richmond et al. (1987), reporting on the same study, estimated that pine voles caused a 78% reduction in crown bark weight and a 56% loss of fibrous roots. Overall, Forshey et al. (1984) estimated losses at \$6,779/ha (\$2,743/acre). Askham (1988) attributed a 36% loss in production in a Washington State apple orchard to damage by montane voles and estimated losses at \$7,500/ha (\$303/acre) in the first year of study.

Control

Cultural and direct lethal measures have been employed to control troublesome populations and make the orchard a less hospitable environment for voles (Silver 1924; Hatt 1930; Eadie 1961; Byers 1985a).

Cultural Techniques and Orchard Management

The fecundity and mobility of voles enable them to repopulate orchards rapidly (Horsfall 1964; Van

Vleck 1968). Miller and Richmond (1983) trapped out all voles from an orchard block in eastern New York during late fall and monitored reinvasion during the subsequent spring, summer, and fall; twice as many trees were infested by voles at the end of the study than before the trapout (Fig. 6). Control programs should focus on altering the orchard environment and reducing its potential for attracting and supporting vole populations.

For the orchardist, ground vegetation is the most important manageable variable affecting vole survival and reproduction; it provides food, concealment from predators, protection from unfavorable weather, and opportunities for reproduction. Ground vegetation reduces soil compaction and erosion and provides protection from vehicular traffic, but it also competes with trees for water and nutrients, harbors insect pests, and provides food and shelter for voles (Forshey 1986). A cover crop is necessary in most orchards, but it must be managed carefully to minimize its suitability as vole habitat. To reduce vole problems, growers maximize benefits and minimize liabilities of orchard cover crops by maintaining a vege-

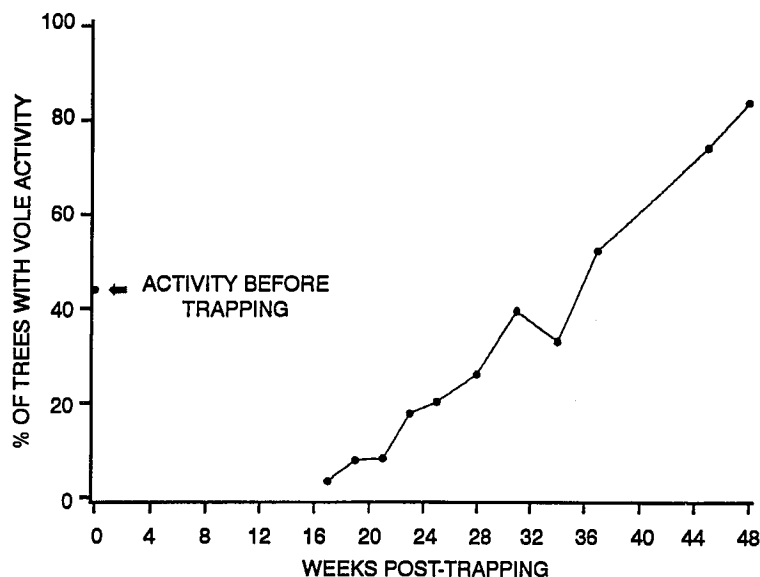


Fig. 6. Rate of pine vole reinvasion of an apple orchard in eastern New York (data from Miller and Richmond 1983).

tation-free zone under the tree canopy and mowing grass alleys between the rows of trees.

A vegetation-free zone under the orchard canopy discourages voles from living near the bases of trees, where they cause the most damage (Holm et al. 1959; Davis 1976; Sullivan and Hogue 1987). For new plantings, growers clear either a 4-foot diameter circle around individual trees or a 4-foot strip along each row of trees (Caslick and Decker 1978). The cleared area is enlarged as the trees grow (Fig. 7). Gravel or cinders are spread on the ground to depress new vegetative growth, although care is taken not to expose previously covered bark, which is highly susceptible to winter injury.

Frequent close mowing of orchard ground cover is one of the best procedures for reducing vole damage (Byers 1985a; Godfrey 1987). Mowing reduces competition for water and nutrients and discourages voles from residing in the orchard. Orchards should be mowed as closely as possible in early spring and thereafter as often as growing conditions dictate (three or more mowings in some areas). Too much delay between mowings results in excessive vegetation which, when cut (especially with a sickle-bar mower), forms a thatch layer that protects voles. A flail or rotary mower is preferred to reduce thatch.

Plant growth regulators might have potential for reducing the frequency with which mowing is required or for retarding growth where mowing is not practical. In a recent study in an eastern Wash-

ington apple orchard (Godfrey 1987), a single application of Embark (diethanolamine salt of mefluidide) reduced late summer undergrowth more than 70% within 10 weeks.

Some investigators have demonstrated adverse effects of toxic or low quality forage on vole growth, reproduction, and survival (Jones 1978; Lewis et al. 1983; Batzli 1985, 1986; Jean and Bergeron 1986; Marquis and Batzli 1989). However, the utility of such plants as orchard ground covers is inconclusive.

Growth form is perhaps the most important consideration in selecting ground cover plants unfavorable to voles (Baker and Brooks 1982). One study in New York demonstrated that vole activity increased with ground cover density, and that little activity occurred below a density of 40% coverage (S. Cantor, Cornell University, Ithaca, N.Y., personal communication). Dense ground covers that mat and form a continuous canopy, such as fescue (*Festuca* sp.) and ryegrass (*Lolium* sp.), support high vole populations (Brooks and Struger 1984). On the other hand, plants with erect, bunch-type growth do not mat or lodge, providing little protective cover for voles. Nicholson and Richmond (1984) suggested buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), curly mesquite (*Hilaria belangeri*), plains reedgrass (*Calamagrostis montanensis*), and several dwarf fescues (*Festuca* spp.) as potential ground covers that reach a short mature height, with reduced mowing requirements and increased light penetration at



Fig. 7. Vegetation-free zone under the canopy dripline discourages voles from living near the bases of trees. Note short, sparse vegetation between tree rows.

ground level. Preliminary field trials in eastern Washington also have identified several dwarf fescues as potentially suitable for reducing vole populations in orchards (L. Askham, Washington State University, personal communication).

Voles also lose favorable conditions if grounds are maintained neatly and apple drops, fallen leaves, prunings, and other debris are removed from the orchard floor. In particular, prunings left in the orchard prevent proper mowing and provide an interim food source for voles and rabbits, which later may eat live trees. Well-traveled roads, moving streams, and buffers of cleared ground or mowed vegetation around the perimeter of orchards slow reinvasion by voles from surrounding areas (Horsfall 1964).

Protective guards placed around the bases of trees preclude girdling of tree trunks by meadow voles, but not girdling of roots by pine voles and montane voles. A cylindrical piece of 1-cm (0.5-

inch) -mesh galvanized hardware cloth (Caslick and Decker 1978) or plastic mesh (Pauls 1986) placed around each tree and set about 10 cm (4 inches) into the ground forms an effective barrier (Fig. 8). Tree guards should be large enough to allow for 5 years of growth and should extend above snow level. Rolled roofing, aluminum foil, sheet metal, and plastic spiral wraps also have been used as tree guards, although none of these is as effective as galvanized hardware cloth (Caslick and Decker 1978). A short life span, difficulty in forming a permanent, tight seal, and harborage of insect pests are major drawbacks to many of the alternative tree guards.

Creosote oil-coal tar mixtures, lime-sulphur solutions, and other concoctions were once common treatments to be applied directly to the bark of trees to deter girdling by voles (Silver 1924; Hatt 1930). However, such repellents may injure trees and rarely remain effective for the entire

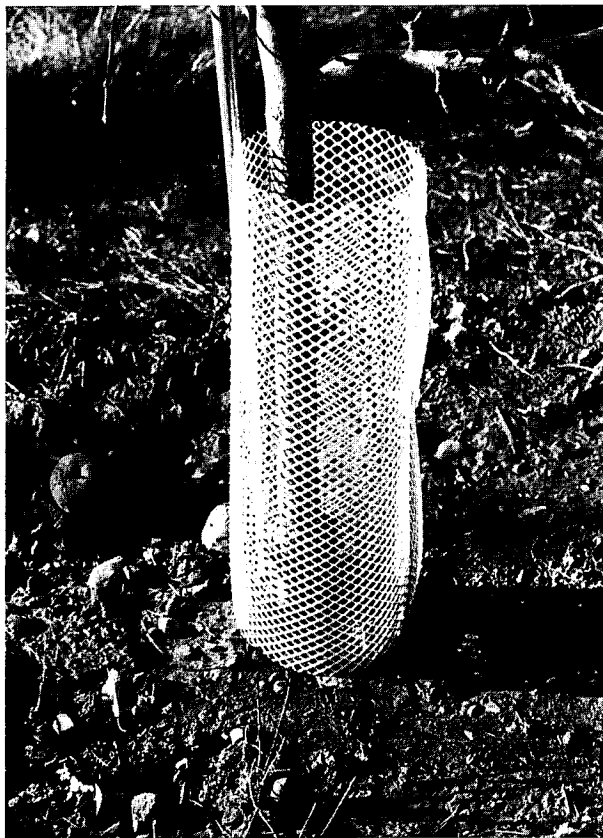


Fig. 8. Plastic mesh cylinder prevents meadow voles from girdling the trunks of trees.

winter (Eadie 1950). Thus, their use has declined. Capsaicin (derived from hot peppers) and thiram (tetramethylthiuram disulfide) currently are registered as dormant season repellents for protecting fruit-bearing trees from deer, rabbits, and voles. However, little has been done to evaluate their efficacy against voles in orchards. Thiram repelled captive voles under experimental conditions (Luke and Snetsinger 1975; Swihart 1990). Methiocarb (a carbamate compound) and quebracho (a condensed tannin) are two experimental repellents that also have reduced girdling by captive voles (Swihart 1990). Predator odors may also be effective vole repellents. Sullivan et al. (1988a, 1988b) reduced vole activity in apple orchards by placing compounds from the anal glands, feces, and urine of ermines (*Mustela erminea*) and red foxes (*Vulpes vulpes*) in slow-release capillary tubes at the bases of trees. Using predator odors to control voles is still in an experimental stage, however, and such products are not yet commercially available.

Development of vole-resistant cultivars and rootstocks is another promising avenue for research (Byers and Cummins 1977; Geyer and Cummins 1980; Wysolmerski et al. 1980). One particular rootstock, Novole, showed resistance to girdling by captive voles (Cummins et al. 1983, 1984), although these findings have not been verified in field trials.

Growers sometimes repair girdled trees by bridge grafting—using a stem or shoot to join the portions of the tree above and below the damage—or inarching—grafting the tops of one or more young trees to the damaged tree above the wound (Silver 1924; Hatt 1930; Hamilton 1938; Eadie 1961). Grafting is labor-intensive, especially for older trees, and may not be practical in orchards with extensive damage. Moreover, voles sometimes girdle bridge grafts in preference to older trunks.

Monitoring Techniques and Action Thresholds

Even well managed orchards are susceptible to invasion and damage by voles, and growers need reliable monitoring techniques that enable them to act quickly and reduce troublesome populations before appreciable damage occurs. The simplest way to detect the presence of voles is to observe runways, burrow openings, girdled trees, or other signs of vole activity. However, although such signs may persist, they can be misleading because voles may have died or emigrated from the area. The apple-slice index is a more reliable indicator of current vole activity (Byers 1975). A slice or portion of apple is placed in a runway or burrow opening or under a roofing shingle, piece of tar paper, or similar cover under the canopy of each tree, and checked 24 h later. The proportion of apple slices that are partly eaten, missing, or otherwise disturbed by voles indicates the percentage of trees infested by voles.

The economic threshold for controlling damage by voles is low; the loss of even one tree is costly and unacceptable if it can be prevented (Byers 1985a). A single animal can cause appreciable damage or even loss of a tree. Thus, controls should be applied wherever voles are present or damage is expected. Many growers implement preventive control programs and regularly apply controls regardless of the level of vole infestation (Caslick and Decker 1978; Byers 1985a).

Lethal Techniques

Rodenticides are an important and necessary component of most control programs because they provide the quickest and most practical means of controlling large populations of voles. Several rodenticides are registered for control of voles in apple orchards (Table 2).

Rodenticide Ground Sprays

Rodenticides sometimes are applied as sprays to vegetation on the orchard floor. The voles then ingest the toxicant in feeding or while grooming themselves after rubbing against the vegetation (Horsfall 1956; Eadie 1961; Horsfall et al. 1974). Endrin formerly was used as a ground spray in apple orchards, but today chlorophacinone is the only rodenticide registered for this purpose. Although ground sprays have been used effectively to control voles, results were not consistent (Stebblein and Richmond 1982; Byers 1985b). Formulations of chlorophacinone applied as ground sprays require 100–400 times as much active ingredient per acre as pelleted formulations of the same toxicant, and thus probably are not cost-effective (Byers 1985b).

Rodenticide Baits

Rodenticides for vole control are most commonly applied to food baits, which can be highly effective when used properly. Baits that have received wide use, either presently or in the past, include fresh fruits and vegetables (e.g., apples and carrots), grains (e.g., corn, oats, and wheat), and synthetic pellets.

Growers must select an appropriate type of bait to apply. Pelleted baits are increasingly used to control voles in apple orchards. Although fresh

fruits and vegetables are highly attractive foods to voles, their use is declining because they are perishable and require more time to prepare and apply. Cracked corn, a widely used bait, is available commercially, relatively inexpensive, easy to store, and readily applied with either aerial or mechanical spreaders. Unfortunately, cracked corn is one of the least effective baits for controlling voles (Merson and Byers 1981; Byers et al. 1982; Hunter 1986; Hunter et al. 1987). Cracked corn baits also may be hazardous to pheasants and other ground-feeding birds (Hayne 1951). Although pelleted formulations of zinc phosphide and anticoagulants usually are more expensive than grain baits, the increased control achieved with these baits often renders their use more cost-effective (Byers 1978, 1979, 1981; Byers et al. 1982).

Resistance and Bait Shyness

Unfortunately, rodenticide baits have not always given consistent or satisfactory control of voles (Fisher 1976; Byers et al. 1982; Steblein and Richmond 1982; Steblein et al. 1983). Many factors influence efficacy, including type of toxicant, attractiveness of the bait carrier, timing and method of application, and past history of rodenticide use.

Rodenticides are classified as either acute or chronic. Acute rodenticides, of which zinc phosphide is the only one registered for use in apple orchards, are fast-acting poisons that usually require only a single feeding to achieve a lethal dose. Toxicosis occurs within a matter of hours, and a relatively small amount of bait usually is sufficient to quickly reduce the size of a large population. In contrast, chronic rodenticides,

Table 2. *Some commercial rodenticides registered for controlling voles in apple orchards.*^a

Active ingredient	Product	Formulation	Proprietor
Zinc phosphide ^b	Hopkins Zinc Phosphide Pellets	Pellet	Haco, Inc.
	Ridall—Zinc	Pellet	Liphatech, Inc.
	Vole Bait Containing Zinc Phosphide	Granular	R&M Exterm Inc.
	Zinc Phosphide Mouse Bait	Granular	FMC Corp.
	ZP Rodent Bait AG	Pellet	Bell Laboratories, Inc.
Chlorophacinone	Rozol Paraffinized Pellets	Pellet	Liphatech, Inc.
	Rozol Rodenticide Ground Spray	Emulsifiable concentrate	Liphatech, Inc.
Diphacinone	Ramik Brown	Pellet	Haco, Inc.

^a Rodenticide registrations vary among states, and it is best to check with local authorities before applying.

^b All zinc phosphide are restricted-use pesticides that may be only by certified pesticide applicators.

which include most anticoagulants, require multiple feedings, often over a period of several days, before animals consume a lethal dose. The anticoagulant baits chlorophacinone and diphacinone are commonly used to control voles in apple orchards.

Many rodenticides lose their effectiveness with repeated and continued use. After several generations, differential survival of voles can lead to the development of populations that are physiologically resistant to the effects of the toxicant. The repeated use of endrin in orchards in Maryland and New York resulted in populations that were as much as 12 times as tolerant to the effects of this poison as were voles from orchards with no history of endrin use (Webb and Horsfall 1967; Forbes 1972; Webb et al. 1973). The use of endrin for pest control no longer is permitted in the United States.

Poison baits also can lose their effectiveness when bait shyness develops, a behavioral process by which animals that ingest sublethal doses learn to avoid the bait during future encounters. Because bait shyness occurs mainly with acute toxicants, growers should not apply zinc phosphide baits more often than once every 6 months (Howard et al. 1977; Sridhara and Srihari 1980). Growers can reduce the pest population with an initial application of a zinc phosphide bait (Table 2), and then 48 h later conduct an apple-slice index to assess the need for a follow-up application with an anticoagulant bait (Table 2). Bait shyness has not been observed with anticoagulants, presumably because more time is required for the onset of toxicosis.

Application Techniques

Baits most commonly are broadcast across the orchard floor by airplane, tractor-mounted spreader, or hand. Zinc phosphide baits generally are broadcast at the rate of 4.5–11.2 kg/ha (4–10 pounds per acre), and chlorophacinone and diphacinone are broadcast at the rate of 11.2–22.4 kg/ha (10–20 pounds per acre). As noted on product labels, mowing ground vegetation and removing leaves before application ensures that broadcast baits reach the ground surface where voles can find them (Hunter 1986; Hunter et al. 1987). To reduce hazards to nontarget animals, label instructions prohibit exposing bait on bare ground, such as within the cleared drip-line. Baiting ditch banks, fencerows, and noncrop areas

around the perimeter of orchards reduces reinvasion of voles into orchards.

Pine voles are not as active aboveground and do not travel as far as meadow voles or montane voles. Therefore, placing bait directly in runways and burrow openings at two to four locations under infested trees is more effective for this species. Label instructions for hand baiting with zinc phosphide baits recommend placing one teaspoon of bait at each spot, allowing a maximum application of 4.5 kg/ha (4 pounds per acre). Label instructions for hand baiting with anticoagulant baits recommend 42 g (1.5 ounces) per placement, allowing a maximum of 11.2 kg/ha (10 pounds per acre). Placing a roofing shingle, board, or other object over the bait at each placement site helps to attract voles to the bait. Pulling overhanging grass back into place also increases bait acceptance.

Frequent and unpredictable rain and snowfall severely limit the life span of baits openly exposed on the orchard floor. Likewise, snow and adverse weather often preclude applying baits during winter when most damage occurs and when voles are most likely to eat bait because of the shortage of preferred foods. An effective method of protecting bait from the elements helps in controlling vole populations.

Growers use a variety of materials to protect baits in orchards, including jars, metal cans, and homemade wooden bait stations (Silver 1924). Tar paper, wooden roofing shakes, shingles, split automobile tires, and other objects placed over baits not only provide protection from rain and snow, but also attract voles to the bait. In areas of high wind velocity, tar paper and other light materials often are secured with a nail. Unfortunately, baits absorb moisture when placed directly on the ground under such protective covers, and generally do not persist more than 2 weeks. Radvanyi (1974), Siddiqi et al. (1984), and Tobin and Richmond (1987) used hollow galvanized metal or PVC (polyvinyl-chloride) tubes joined in the shape of an inverted "T"; bait was placed in the vertical tube, and voles entered the horizontal tubes to consume bait. A cover over the top of the vertical tube protected the bait from rain and snow. The stations were constructed tall enough to extend above vegetation and snow accumulations, and were secured to the trees to allow relocation and prevent disturbance by farm equipment. Because of the potential for bait shyness, acute toxicants were not placed in bait stations for extended periods.

Time of Application

Time of application was found important in achieving control with rodenticides. Growers apply baits only when they anticipate several days of dry weather. Vole baits are most effective when naturally occurring and preferred foods are scarce. Toxic bait acceptance is diminished in the presence of fresh green vegetation, abundant apple drops, and other naturally occurring foods. Regulations listed on the registration labels for use of registered toxicants stipulate that baits should be applied only during the dormant season, after harvest, and before bud burst the following spring. Late fall is a critical time to bait because it may be the last opportunity to reduce populations before the onset of winter, when snow cover can preclude rodenticide use. Even where control is achieved in fall, voles often reinvade orchards and cause substantial damage under the protective cover snow. Thus, growers monitor orchards for signs of recent vole activity and apply baits where necessary. Evidence of reinvansion is conspicuous during snowmelt because trails are readily apparent. Furthermore, the shortage of preferred foods at time of snowmelt greatly enhances the acceptance of rodenticide baits (Fitch 1954). When winter survival is high, signs of vole activity usually are abundant in spring, and growers generally apply baits to reduce vole populations before onset of the breeding season. Spring baiting is most effective if conducted before renewed growth of the orchard ground vegetation diminishes bait acceptance (Tobin, unpublished data).

Trapping

Traps occasionally are effective in reducing pest populations in localized situations, such as small orchards with sparse populations. However, trapping is impractical in large orchards with dense populations because of costs of labor and materials.

Biological Control

Biological control is an appealing, but rarely effective, form of vertebrate control. Numerous birds and mammals prey on voles, but seldom reduce pest populations to the low levels necessary for control purposes (Howard 1967). Most predators have broad-based diets that allow them to switch to alternative, more easily caught prey when vole populations decline. Thus, predators, even when effective, usually leave residual pest populations in orchards. In certain situations, predators may help to delay, but not prevent, the increase of rodent populations that already have been reduced to low levels (Maher 1967; Pearson 1964, 1971; MacLean et al. 1974; Fitzgerald 1977; Newsome 1990).

An Integrated Approach

Many factors influence fluctuations of vole populations (Fig. 9). Implementing an effective control program requires a variety of strategies to eliminate or reduce factors that contribute to increases. Rodenticides alone are rarely sufficient for long-term control. Legal restrictions and unpredictable weather often preclude application of rodenticides until after pest populations have be-

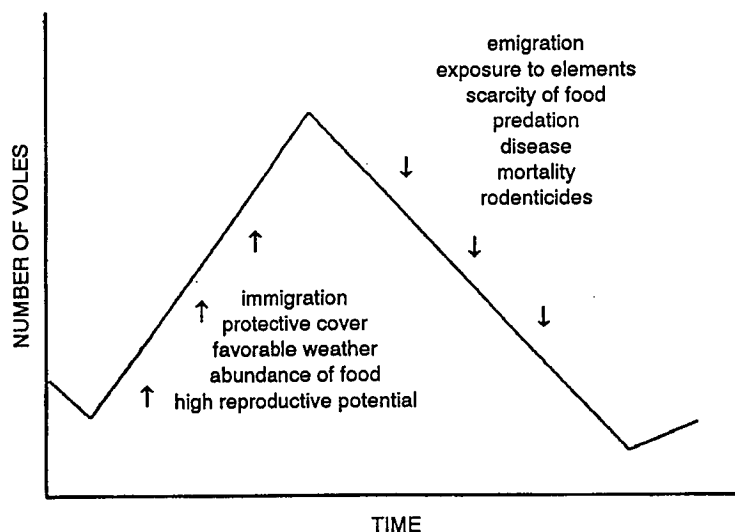


Fig. 9. Factors that influence irruption and decline of vole populations.

come epidemic and significant damage has occurred. Even where toxic baits provide control, populations frequently build rapidly. Thus, growers must modify the orchard environment to reduce the invasion, reproduction, and survival of voles. Frequent and close mowing of ground vegetation during the growing season and establishment of a vegetation-free zone under the dripline of the trees reduces the availability of foods preferred by voles, removes cover that protects them from predation, and exposes the animals to the seasonal elements. Where meadow voles are the species of concern, wrapping 1-cm (0.5-inch)-mesh galvanized hardware cloth around the base of trees prevents girdling. Periodic inspection of orchards provides an early warning of reinvasion or repopulation and allows control measures to be applied before vole populations increase significantly. Allowing voles to freely multiply increases the probability of damage to trees, renders future control more difficult, and can necessitate the introduction of greater amounts of poisonous bait into the environment. When vole populations build, proper use of toxic baits is the quickest and most effective control method.

Acknowledgments

C. Forshey, C. Webster, and two anonymous reviewers commented on earlier drafts of this manuscript. T. Sayre furnished the cover illustration and the three line drawings of voles.

References

- Ambrose, H. W., III. 1973. An experimental study of some factors affecting the spatial and temporal activity of *Microtus pennsylvanicus*. *Journal of Mammalogy* 54:79-110.
- Anthony, R. G., D. A. Simpson, G. M. Kelly, and G. L. Storm. 1986. Dynamics of pine vole populations in two Pennsylvania orchards. *American Midland Naturalist* 116:108-117.
- Askham, L. R. 1988. A two year study of the physical and economic impact of voles (*Microtus montanus*) on mixed maturity apple (*Malus* spp.) orchards in the Pacific northwestern United States. *Proceedings of the Vertebrate Pest Conference* 13:151-155.
- Bailey, V. 1924. Breeding, feeding, and other life habits of meadow mice (*Microtus*). *Journal of Agricultural Research* 27:523-535.
- Baker, J. A., and R. J. Brooks. 1982. Impact of raptor predation on a declining vole population. *Journal of Mammalogy* 63:297-300.
- Banks, R. C., R. W. McDiarmid, and A. L. Gardner. 1987. Checklist of vertebrates of the United States, the U.S. territories, and Canada. U.S. Fish and Wildlife Service Resource Publication 166. 79 pp.
- Batzli, G. O. 1985. Nutrition. Pages 779-811 in R. H. Tamarin, editor. *Biology of New World Microtus*. American Society of Mammalogists Special Publication 8.
- Batzli, G. O. 1986. Nutritional ecology of the California vole: effects of food quality on reproduction. *Ecology* 67:406-412.
- Benton, A. H. 1955. Observations on the life history of the northern pine mouse. *Journal of Mammalogy* 36:52-62.
- Berger, P. J., N. C. Negus, and C. N. Rowsemitt. 1987. Effect of 6-methoxybenzoxazolinone on sex ratio and breeding performance in *Microtus montanus*. *Biology of Reproduction* 36:255-260.
- Berger, P. J., N. C. Negus, E. H. Sanders, and P. D. Gardner. 1981. Chemical triggering of reproduction in *Microtus montanus*. *Science* 214:69-70.
- Brooks, R. J., and S. A. Struger. 1985. Relationship between seasonal changes in forage quality and feeding patterns in meadow voles (*Microtus pennsylvanicus*). *Proceedings of the Eastern Wildlife Damage Control Conference* 2:60-65.
- Burt, W. H., and R. P. Grossenheider. 1976. A field guide to the mammals. Houghton Mifflin Co., Boston, Mass. 289 pp.
- Byers, R. E. 1974. Pine mouse control in apple orchards. *Mountaineer Grower* 335. 13 pp.
- Byers, R. E. 1975. A rapid method for assessing pine vole control in orchards. *HortScience* 10:391-392.
- Byers, R. E. 1978. Performance of rodenticides for the control of pine voles in orchards. *Journal of the American Society for Horticultural Science* 103:65-69.
- Byers, R. E. 1979. Meadow vole control using anticoagulant baits. *HortScience* 14:44-45.
- Byers, R. E. 1981. Pine vole control with anticoagulant baits in apple orchards. *Journal of the American Society for Horticultural Science* 106:101-105.
- Byers, R. E. 1984. Control and management of vertebrate pests in deciduous orchards in the eastern United States. *Horticultural Reviews* 6:253-285.
- Byers, R. E. 1985a. Management and control. Pages 621-646 in R. H. Tamarin, editor. *Biology of New World Microtus*. American Society of Mammalogists Special Publication 8.
- Byers, R. E. 1985b. Ground cover sprays versus baiting for the control of microtine rodents. *Acta Zoologica Fennica* 173:173-174.
- Byers, R. E., and J. N. Cummins. 1977. Variations in susceptibility of apple stems to attack by pine voles. *Journal of the American Society for Horticultural Science* 102:201-203.
- Byers, R. E., M. H. Merson, and S. D. Palmateer. 1982. Control of orchard voles with broadcast baits. *Journal*

- of the American Society for Horticultural Science 107:613-619.
- Caslick, J. W., and D. J. Decker. 1978. Orchard mouse control. Cornell University Conservation Circular 16(5). 14 pp.
- Cengel, D. J., J. E. Estep, and R. L. Kirkpatrick. 1978. Pine vole reproduction in relation to food habits and body fat. *Journal of Wildlife Management* 42:822-833.
- Chitty, D. 1960. Population processes in the vole and their relevance to general theory. *Canadian Journal of Zoology* 38:99-113.
- Cummins, J. N., H. S. Aldwinckle, and R. E. Byers. 1983. "Novole" apple. *HortScience* 18:772-774.
- Cummins, J. N., H. S. Aldwinckle, and R. E. Byers. 1984. Novole, an apple stock resistance to voles and other environmental hazards. *Fruit Varieties Journal* 38:58-60.
- Davis, D. E. 1976. Management of pine voles. *Proceedings of the Vertebrate Pest Conference* 7:270-275.
- Dobson, F. S., and P. Myers. 1989. The seasonal decline in the litter size of meadow voles. *Journal of Mammalogy* 70:142-152.
- Douglass, R. J. 1976. Spatial interactions and microhabitat selections of two locally sympatric voles, *Microtus montanus* and *Microtus pennsylvanicus*. *Ecology* 57:346-352.
- Eadie, W. R. 1950. New techniques in control of orchard mice. Cornell University Agricultural Experiment Station Bulletin 856. 16 pp.
- Eadie, W. R. 1961. Control of wildlife damage in orchards. Cornell Extension Bulletin 1055. 16 pp.
- Elton, C. S. 1942. Voles, mice and lemmings: problems in population dynamics. Oxford University Press, London. 496 pp.
- Fisher, A. R. 1976. Relationships between soils and pine vole (*Microtus pinetorum*) populations in Pennsylvania orchards. M.S. thesis, Pennsylvania State University, State College, Pa. 57 pp.
- Fitch, H. S. 1954. Seasonal acceptance of bait by small mammals. *Journal of Mammalogy* 35:39-47.
- FitzGerald, B. M. 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. *Journal of Animal Ecology* 46:367-397.
- FitzGerald, R. W., and D. M. Madison. 1983. Social organization of a free-ranging population of pine voles, *Microtus pinetorum*. *Behavioral Ecology and Sociobiology* 13:183-187.
- Forbes, J. E. 1972. The New York pine vole situation. Pages 4-13 in J. E. Forbes, editor. *Proceedings of the New York Pine Mouse Symposium*. U.S. Bureau of Sport Fisheries and Wildlife, Albany, N.Y.
- Forshey, C. G. 1986. An overview of orchard cover crop management. *Proceedings of the Washington State Horticultural Association* 82:125-128.
- Forshey, C. G., P. N. Miller, and M. E. Richmond. 1984. Effects of differential pine vole populations on growth and yield of "McIntosh" apple trees. *HortScience* 19:820-822.
- Gates, J. E., and D. M. Gates. 1980. A winter food cache of *Microtus pennsylvanicus*. *American Midland Naturalist* 103:407-408.
- Gentry, J. B. 1968. Dynamics of an enclosed population of pine mice, *Microtus pinetorum*. *Researches on Population Ecology (Kyoto)* 10:21-30.
- Getz, L. L. 1960. A population study of the vole, *Microtus pennsylvanicus*. *American Midland Naturalist* 64:392-405.
- Getz, L. L. 1961. Home ranges, territoriality, and movement of the meadow vole. *Journal of Mammalogy* 42:24-36.
- Geyer, L. A., and J. N. Cummins. 1980. Textural and taste influences on gnawing by pine voles. *Proceedings of the Eastern Pine and Meadow Vole Symposium* 4:43-49.
- Godfrey, M. E. R. 1987. Cultural practices affecting montane voles in Washington apple orchards. Pages 127-138 in C. G. J. Richards and T. Y. Ku, editors. *Control of mammal pests*. Taylor & Francis, New York, N.Y.
- Goertz, J. W. 1971. An ecological study of *Microtus pinetorum* in Oklahoma. *American Midland Naturalist* 86:1-12.
- Gourley, R. S. 1983. Demography of *Microtus pinetorum*. Ph.D. thesis, Cornell University, Ithaca, N.Y. 111 pp. + appendix.
- Hamilton, W. J., Jr. 1937. Activity and home range of the field mouse, *Microtus pennsylvanicus pennsylvanicus* (Ord.). *Ecology* 18:255-263.
- Hamilton, W. J., Jr. 1938. Life history notes on the northern pine mouse. *Journal of Mammalogy* 19:163-170.
- Hasler, J. F. 1975. A review of reproduction and sexual maturation in the microtine rodents. *Biologist* 57:52-86.
- Hatt, R. T. 1930. The biology of the voles of New York. *Roosevelt Wild Life Bulletin* 5:513-623.
- Hayne, D. W. 1951. Zinc phosphide: its toxicity to pheasants and effect of weathering upon its toxicity to mice. *Michigan Quarterly Bulletin* 33:412-425.
- Hestbeck, J. B. 1986. Multiple regulation states in populations of the California vole, *Microtus californicus*. *Ecological Monographs* 56:161-181.
- Hoffmann, R. S., and J. W. Koepl. 1985. Zoogeography. Pages 84-115 in R. H. Tamarin, editor. *Biology of new world Microtus*. American Society of Mammalogists Special Publication 8.
- Holm, L., F. A. Gilbert, and E. Haltvick. 1959. Elimination of rodent cover adjacent to apple trees. *Weeds* 7:405-408.
- Horsfall, F., Jr. 1956. Pine mouse control with ground-sprayed endrin. *Proceedings of the American Society for Horticultural Science* 67:68-74.
- Horsfall, F., Jr. 1963. Observations on fluctuating pregnancy rate of pine mice and mouse feed potential in Virginia orchards. *Proceedings of the American Society for Horticultural Science* 83:276-279.

- Horsfall, F., Jr. 1964. Pine mouse invasion and reinfestation of orchards subsequent to removal of adjacent woody plant cover or the use of ground sprays. *Proceedings of the American Society for Horticultural Science* 85:161-171.
- Horsfall, F., Jr., R. E. Webb, and R. E. Byers. 1974. Dual role of forbs and rodenticides in the ground spray control of pine mice. *Proceedings of the Vertebrate Pest Conference* 6:112-126.
- Howard, W. E. 1967. Biological control of vertebrate pests. *Proceedings of the Vertebrate Pest Conference* 3:137-157.
- Howard, W. E., R. E. Marsh, and R. E. Cole. 1977. Duration of associative memory to toxic bait in deer mice. *Journal of Wildlife Management* 41:484-486.
- Hunter, R. E. 1986. Controlling mice successfully depends on bait placement. *Goodfruit Grower* 37:37.
- Hunter, R. E., L. R. Askham, and M. E. R. Godfrey. 1987. The effectiveness of five rodenticides and three application procedures in controlling microtine voles (*Microtus montanus*) in Washington state apple orchards. *Crop Protection* 6:277-279.
- Innes, D. G. L. 1978. A reexamination of litter size in some North American microtines. *Canadian Journal of Zoology* 56:1488-1496.
- Jannett, F. J., Jr. 1977. On the sociobiology of the montane vole, *Microtus montanus nanus* (Rodentia: Muridae). Ph.D. thesis, Cornell University, Ithaca, N.Y. 167 pp.
- Jannett, F. J., Jr. 1980. Social dynamics of the montane vole *Microtus montanus* as a paradigm. *Biologist* 62:3-19.
- Jannett, F. J., Jr. 1982. Nesting patterns of adult voles *Microtus montanus* in field populations. *Journal of Mammalogy* 63:495-498.
- Jannett, F. J., Jr. 1984. Reproduction of the montane vole, *Microtus montanus*, in subnivean populations. *Carnegie Museum of Natural History Special Publication* 10:215-223.
- Jean, Y., and J.-M. Bergeron. 1986. Can voles (*Microtus pennsylvanicus*) be poisoned by secondary metabolites of commonly eaten foods? *Canadian Journal of Zoology* 64:158-162.
- Johnson, M. L., and S. Johnson. 1982. Voles. Pages 326-354 in J. A. Chapman and G. A. Feldhamer, editors. *Wild mammals of North America: biology, management, and economics*. Johns Hopkins University Press, Baltimore, Md.
- Jones, E. N. 1978. Influences of crownvetch (*Coronilla varia* L.) on the density and spatial distribution of the meadow vole (*Microtus pennsylvanicus*). M.S. thesis, Pennsylvania State University, State College. 52 pp.
- Koplin, J. R., and R. S. Hoffmann. 1968. Habitat overlap and competitive exclusion in voles (*Microtus*). *American Midland Naturalist* 80:494-507.
- Korn, H., and M. J. Taitt. 1987. Initiation of early breeding in a population of *Microtus townsendii* (Rodentia) with the secondary plant compound 6-MBOA. *Oecologia* 71:593-596.
- Lewis, E., D. H. Rhodes, and M. Richmond. 1983. Acceptability of six candidate groundcovers to meadow voles. *Proceedings of the Eastern Pine and Meadow Vole Symposium* 7:87-92.
- Luke, J. E., and R. J. Snetsinger. 1975. Apple trees protected from voles with thiram. *Science in Agriculture* 23:7.
- MacLean, S. F., Jr., B. M. Fitzgerald, and F. A. Pitelka. 1974. Population cycles in arctic lemmings: winter reproduction and predation by weasels. *Arctic and Alpine Research* 6:1-12.
- Madison, D. M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioral Ecology and Sociobiology* 7:65-71.
- Madison, D. M. 1984. Group nesting and its ecological and evolutionary significance in overwintering microtine rodents. Pages 267-274 in J. F. Merritt, editor. *Winter ecology of small mammals*. Carnegie Museum of Natural History Special Publication 10.
- Madison, D. M. 1985. Activity rhythms and spacing. Pages 373-419 in R. H. Tamarin, editor. *Biology of New World Microtus*. American Society of Mammalogists Special Publication 8.
- Madison, D. M., R. W. FitzGerald, and W. J. McShea. 1984. Dynamics of social nesting in overwintering meadow voles (*Microtus pennsylvanicus*): possible consequences for population cycling. *Behavioral Ecology and Sociobiology* 15:9-17.
- Madison, D. M., and W. J. McShea. 1987. Seasonal changes in reproductive tolerance, spacing, and social organization in meadow voles: a microtine model. *American Zoologist* 27:899-908.
- Maher, W. J. 1967. Predation by weasels on a winter population of lemmings, Banks Island, Northwest Territories. *Canadian Field-Naturalist* 81:248-250.
- Marquis, R. J., and G. O. Batzli. 1989. Influence of chemical factors on palatability of forage to voles. *Journal of Mammalogy* 70:503-511.
- McGuire, B., and M. Novak. 1986. Parental care and its relationship to social organization in the montane vole (*Microtus montanus*). *Journal of Mammalogy* 67:305-311.
- McShea, W. J., and D. M. Madison. 1989. Measurements of reproductive traits in a field population of meadow voles. *Journal of Mammalogy* 70:132-141.
- Meade, J. B. 1975. Food selection and turnover of nitrogen, phosphorus, and potassium by *Microtus pennsylvanicus*. Ph.D. thesis, Cornell University, Ithaca, N.Y. 130 pp. + appendix.
- Merson, M. H., and R. E. Byers. 1981. Laboratory efficacy of some commercial zinc phosphide baits used for control of meadow and pine voles in orchards. *HortScience* 16:49-51.
- Miller, D. H., and L. L. Getz. 1969. Life-history notes on *Microtus pinetorum* in central Connecticut. *Journal of Mammalogy* 50:777-784.

- Miller, P. N., and M. E. Richmond. 1983. Movements of the pine vole (*Microtus pinetorum*) in repopulating orchard habitat. Proceedings of the Eastern Wildlife Damage Control Conference 1:231-234.
- Negus, N. C., and P. J. Berger. 1977. Experimental triggering of reproduction in a natural population of *Microtus montanus*. Science 196:1230-1231.
- Negus, N. C., P. J. Berger, and L. G. Forslund. 1977. Reproductive strategy of *Microtus montanus*. Journal of Mammalogy 58:347-353.
- Negus, N. C., and A. J. Pinter. 1965. Litter sizes of *Microtus montanus* in the laboratory. Journal of Mammalogy 46:434-437.
- Newsome, A. 1990. The control of vertebrate pests by vertebrate predators. Trends in Ecology and Evolution 5:187-191.
- Nicholson, A. G., and M. E. Richmond. 1984. Considering vole habitat preferences in living mulch research. Proceedings of the Eastern Pine and Meadow Vole Symposium 8:52-60.
- Oliveras, D., and M. Novak. 1986. A comparison of paternal behaviour in the meadow vole *Microtus pennsylvanicus*, the pine vole *M. pinetorum* and the prairie vole *M. ochrogaster*. Animal Behaviour 34:519-526.
- Ostfeld, R. S., S. R. Pugh, J. O. Seamon, and R. H. Tamarin. 1988. Space use and reproductive success in a population of meadow voles. Journal of Animal Ecology 57:385-394.
- Paul, J. R. 1970. Observations on the ecology, populations and reproductive biology of the pine vole, *Microtus pinetorum*, in North Carolina. Illinois State Museum Reports of Investigations 20. 28 pp.
- Pauls, R. W. 1986. Protection with Vexar cylinders from damage by meadow voles of tree and shrub seedlings in northeastern Alberta. Proceedings of the Vertebrate Pest Conference 12:199-204.
- Pearson, K., and C. G. Forshey. 1978. Effects of pine vole damage on tree vigor and fruit yield in New York apple orchards. HortScience 13:56-57.
- Pearson, K. J. 1976. Some economic aspects of pine vole damage in apple orchards of New York State. M.S. thesis, State University of New York, Syracuse. 54 pp.
- Pearson, O. P. 1964. The prey of carnivores during one cycle of mouse abundance. Journal of Animal Ecology 35:217-233.
- Pearson, O. P. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy 52:41-49.
- Phillips, M., C. G. Forshey, G. B. White, and M. E. Richmond. 1987. The economic impact of wildlife damage on Hudson Valley orchards. Proceedings of the Eastern Wildlife Damage Control Conference 3:66-82.
- Piper, S. E. 1909. The Nevada mouse plague of 1907-08. U.S. Department of Agriculture Farmers' Bulletin 352. 23 pp.
- Pitelka, F. A. 1957. Some aspects of population structure in the short-term cycle of the brown lemming in northern Alaska. Cold Spring Harbor Symposia on Quantitative Biology 22:237-251.
- Radvanyi, A. 1974. Small mammal census and control on a hardwood plantation. Proceedings of the Vertebrate Pest Conference 6:9-19.
- Renzullo, P. O., and M. E. Richmond. 1982. Status of winter populations of pine voles (*Microtus pinetorum*). Proceedings of the Pine and Meadow Vole Symposium 6:62-66.
- Richmond, M. E., C. G. Forshey, L. A. Mahaffy, and P. N. Miller. 1987. Effects of differential pine vole populations on growth and yield of "McIntosh" apple trees. Proceedings of the Eastern Wildlife Damage Control Conference 3:296-304.
- Sanders, E. H., P. D. Gardner, P. J. Berger, and N. C. Negus. 1981. 6-Methoxybenzoxazolinone: a plant derivative that stimulates reproduction in *Microtus montanus*. Science 214:67-69.
- Schadler, M. H., and G. M. Butterstein. 1979. Reproduction in the pine vole, *Microtus pinetorum*. Journal of Mammalogy 60:841-844.
- Siddiqi, Z., D. Blaine, and S. Taylor. 1984. Meadow vole control in Ontario apple orchards. Proceedings of the Eastern Wildlife Damage Control Conference 1:207-208.
- Silver, J. 1924. Mouse control in field and orchard. U.S. Department of Agriculture Farmers' Bulletin 1397. 14 pp.
- Sridhara, S., and K. Srihari. 1980. Zinc phosphide and vacor induced bait shyness and its persistence in *Mus platythrix*. Proceedings of the Indian Academy of Sciences 89:221-225.
- Stebblein, P. F., P. N. Miller, and M. E. Richmond. 1983. Efficacy of spring broadcast rodenticides in the Hudson Valley, New York. Proceedings of the Eastern Pine and Meadow Vole Symposium 7:19-24.
- Stebblein, P. F., and M. E. Richmond. 1982. Rodenticide evaluation in the Hudson Valley during 1980 and 1981. Proceedings of the Eastern Pine and Meadow Vole Symposium 6:33-38.
- Stockrahm, D. M. B. 1985. Effect of habitat on the population ecology of voles (*Microtus pinetorum* and *M. pennsylvanicus*) coexisting in apple orchards. Ph.D. thesis, Ohio State University, Columbus. 298 pp.
- Stoecker, R. E. 1972. Competitive relations between sympatric populations of voles (*Microtus montanus* and *M. pennsylvanicus*). Journal of Animal Ecology 41:311-329.
- Sullivan, T. P., D. R. Crump, and D. S. Sullivan. 1988a. Use of predator odors as repellents to reduce feeding damage by herbivores. III. Montane and meadow voles (*Microtus montanus* and *Microtus pennsylvanicus*). Journal of Chemical Ecology 14:363-377.
- Sullivan, T. P., and E. J. Hogue. 1987. Influence of orchard floor management on vole and pocket gopher populations and damage in apple orchards. Journal of the American Society for Horticultural Science 112:972-977.

- Sullivan, T. P., D. S. Sullivan, D. R. Crump, H. Weiser, and E. A. Dixon. 1988b. Predator odors and their potential role in managing pest rodents and rabbits. *Proceedings of the Vertebrate Pest Conference* 13:145-150.
- Swihart, R. K. 1990. Quebracho, thiram, and methiocarb reduce consumption of apple twigs by meadow voles. *Wildlife Society Bulletin* 18:162-166.
- Tobin, M. E., and M. E. Richmond. 1987. Bait stations for controlling voles in apple orchards. *Proceedings of the Eastern Wildlife Damage Control Conference* 3:287-295.
- Valentine, G. L., and R. L. Kirkpatrick. 1970. Seasonal changes in reproductive and related organs in the pine vole, *Microtus pinetorum*, in southwestern Virginia. *Journal of Mammalogy* 51:553-560.
- Van Vleck, D. B. 1968. Movements of *Microtus pennsylvanicus* in relation to depopulated areas. *Journal of Mammalogy* 49:92-103.
- Webb, R. E., R. W. Hartgrove, W. C. Randolph, V. J. Petrella, and F. Horsfall, Jr. 1973. Toxicity studies in endrin-susceptible and resistant strains of pine mice. *Toxicology and Applied Pharmacology* 25:42-47.
- Webb, R. E., and F. Horsfall, Jr. 1967. Endrin resistance in the pine mouse. *Science* 156:1762.
- Webster, A. B., and R. J. Brooks. 1981. Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy* 62:738-751.
- Wysolmerski, J. C., R. E. Byers, and J. N. Cummins. 1980. Laboratory evaluation of some *Malus* clones for susceptibility to girdling by pine voles. *Journal of the American Society for Horticultural Science* 105:675-677.